

Naiads (Bivalvia - Hyriidae) in the "Conglomerado osífero" (late Miocene), Entre Ríos Province, Argentina

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NAIADS (BIVALVIA-HYRIIDAE) IN THE "CONGLOMERADO OSÍFERO" (LATE MIOCENE), ENTRE RÍOS PROVINCE, ARGENTINA

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Abstract. The freshwater mussels of the family Hyriidae (Bivalvia) are widespread in the Neotropical region, including several fossil and living species of the genus *Diplodon* Spix. A specimen assigned to *Diplodon* sp., recovered from the "Conglomerado osífero" (late Miocene) at La Toma Vieja, north of Paraná City (Entre Ríos Province, Argentina), is described herein. The report of *Diplodon* sp. in the "Conglomerado osífero" would support the traditional interpretation of a fluvial paleoenvironment for this horizon. This is the first accurate fossil record of the genus for the Entre Ríos Province, extending the occurrence of the family Hyriidae to the late Miocene of the Mesopotamian region.

Key words. Freshwater bivalves. Hyriidae. *Diplodon*. "Conglomerado osífero". Neogene. Entre Ríos. Argentina.

Resumen. NÁYADES (BIVALVIA - HYRIIDAE) EN EL "CONGLOMERADO OSÍFERO" (MIOCENO TARDÍO), ENTRE RÍOS, ARGENTINA. Los mejillones de agua dulce de la familia Hyriidae (Bivalvia) están muy extendidos en la región Neotropical; incluido el género *Diplodon* con varias especies fósiles y actuales. Se describe aquí un espécimen asignado a *Diplodon* sp. recuperado del "Conglomerado osífero" (Mioceno tardío) en La Toma Vieja, al norte de la ciudad de Paraná (provincia de Entre Ríos, Argentina). El reporte de *Diplodon* sp. en el "Conglomerado osífero" apoyaría la interpretación tradicional de un paleoambiente fluvial para este nivel. Además, representa el primer registro fósil exacto del género para la provincia de Entre Ríos, extendiendo la presencia de la familia Hyriidae hasta el Mioceno tardío de la región mesopotámica.

Palabras clave. Bivalvos de agua dulce. Hyriidae. *Diplodon*. "Conglomerado osífero". Neógeno. Entre Ríos. Argentina.

THE NAIADS or "Almejas Nacaríferas", as called by Ageitos de Castellanos (1960), are very common and highly diverse in South America. These freshwater bivalves of the family Hyriidae Swainson, 1840 are represented in this continent by seven genera and approximately 249 species (Torres *et al.*, 2018), distributed from equatorial latitudes to the southern lakes and rivers of Argentinean and Chilean Patagonia (see Ageitos de Castellanos, 1959; Bonetto, 1973). One of the most widespread genus is *Diplodon* Spix in Wagner, 1827 with many fossil and living species (see Torres *et al.*, 2013, 2018; Pérez *et al.*, 2019). Present day, the greatest diversity of *Diplodon* is found in the relatively clear waters of the upper Paraná River (Torres *et al.*, 2013).

In Argentina, *Diplodon* has a long temporal range, from the Middle Jurassic to the present (*e.g.*, Ihering, 1903; Doello Jurado, 1927; Pilsbry & Olsson, 1935; Parodiz, 1969;

Manceñido & Damborenea, 1984; Morton & Herbst, 2001; Parras & Griffin, 2013; Pérez *et al.*, 2019). However, records of *Diplodon* in the Mesopotamian region are relatively scarce (Frenguelli, 1920; Herbst & Camacho, 1970; Morton & Jalfin, 1987; Morton & Sequeira, 1991; Morton, 2004).

Particularly in the Neogene sedimentary sequence of the Entre Ríos Province, the presence of marine bivalves dominates the fossil record (see Pérez *et al.*, 2013), including a few references to the species *Diplodon fraud* Ihering, 1907, attributed to strata of the Paraná Formation, as pointed out by Frenguelli (1920: p. 127). Overlaying the mudstone beds of the Paraná Formation, the "Conglomerado osífero" contains a rich fauna of continental vertebrates, mostly mammals (Cione *et al.*, 2000; Brandoni & Noriega, 2013; Brandoni *et al.*, 2019; Schmidt *et al.*, 2020), in association with scarce remains of continental invertebrates (Frenguelli, 1920: p. 83, 85).

The aims of this study are to report the presence of *Diplodon* sp. in the "Conglomerado osífero" and to discuss its implications.

Institutional abbreviations. CM, Carnegie Museum of Natural History, Pittsburgh, United States of America. DMT-Pi, Colección de Paleoinvertebrados, Centro de Investigación Científica y de Transferencia Tecnológica a la Producción (CICYTTP, CONICET-Prov. ER-UADER), Diamante, Argentina. MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina. MPM-Pi, Museo Regional Provincial "Padre Manuel J. Molina", Río Gallegos, Argentina. PZ-CTES, Museo de la Universidad Nacional del Nordeste, Sección Paleozoología, Corrientes, Argentina. SMF, Senckenberg Museum Frankfurt, Frankfurt, Germany.

MATERIAL AND METHODS

The specimen reported herein, DMT-Pi-536, was collected in the locality "La Toma Vieja" (= Toma Vieja; Brunetto *et al.*, 2013) [31° 42' 09" S, 60° 28' 45" W; Fig. 1.1] (Pérez *et al.*, 2013). Measurements were taken with a micrometer Asimeto

Caliper, according to Cox (1969). Suprageneric classification follows Bieler *et al.* (2010).

GEOLOGICAL SETTING

In the Entre Ríos Province, the "Conglomerado osífero" crops out discontinuously in the vicinity of the city of Paraná along the Paraná river cliffs and many subsidiary streams of the latter, northwards to Hernandarias. The "ossiferous conglomerate" is clearly distinguished from the visible unconformity with the shale beds of the underlying Paraná Formation (Fig. 1.2).

The "Conglomerado osífero" is characterized by levels with fine quartz, clay and chalcedony pebbles, as well as abundant bones and teeth of frequently fragmented and disassociated continental vertebrates and a few mostly-reworked marine ones (Cione *et al.*, 2000). The vertebrate remains are hard, heavy and well mineralized. They are also affected by siliceous and ferruginous cements and are frequently stained by manganese oxides (Frenguelli, 1920; Cione *et al.*, 2000; Brandoni, 2011; Schmidt, 2015). Traditionally, the "Conglomerado osífero" or "Mesopotamiense"

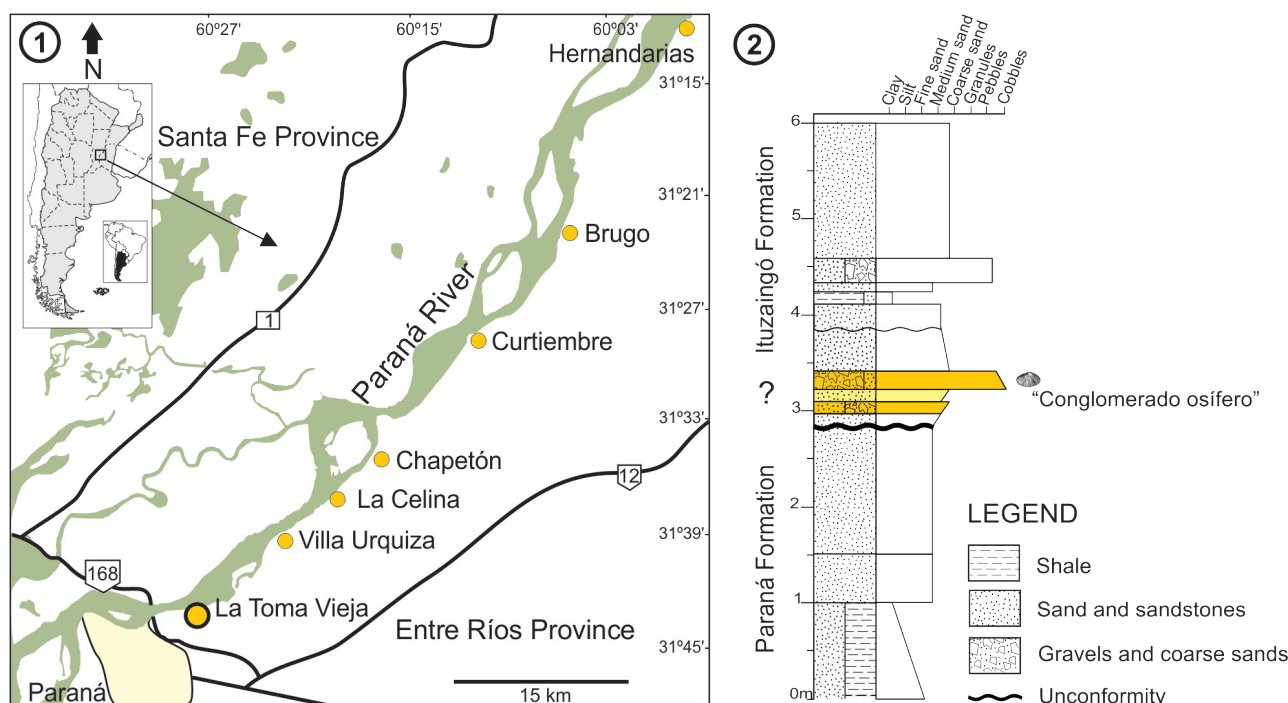


Figure 1. 1, Location of the locality La Toma Vieja in Entre Ríos Province, Argentina. **2,** Stratigraphic section of the locality where the specimen DMT-Pi-536 was collected.

was considered as part of the fluvial Ituzaingó Formation (Frenguelli, 1920; Aceñolaza, 1976, 2000; Brunetto *et al.*, 2013). However, whereas Brunetto *et al.* (2013) regarded the “Conglomerado osífero” as part of the lower member of the Ituzaingó Formation, Pérez (2013a) interpreted it as part of the marine Paraná Formation.

In the absence of any radiometric dating, the age of the “Conglomerado osífero” has been estimated by biostratigraphic correlation to other Neogene units, based on its mammal content. Thus, the age of the “Conglomerado osífero” is mainly interpreted to be Huayquerian (*ca.* 9–6.8 Ma *sensu* Cione *et al.*, 2000), or alternatively to the Chasicoan–Huayquerian lapse (*ca.* 10–6.8/5.3 Ma; Brandoni, 2013), and consequently correlated to the Tortonian–Messinian (late Miocene) (International Chronostratigraphic Chart, 2021). $^{86}\text{Sr}/^{87}\text{Sr}$ dating of mollusks from the underlying Paraná Formation in the locality of Punta Gorda (Diamante, Entre Ríos Province), ranges from 9.47 Ma (Tortonian) (Pérez, 2013b) to 7.55–6.67 Ma (Tortonian–Messinian) (del Río *et al.*, 2018). Considering the relationship between the fauna

of the “Conglomerado osífero” and that of other Neogene units (see Cione *et al.*, 2000; Brandoni, 2013; Schmidt *et al.*, 2020), as well as the proposed age for the Paraná Formation (see Pérez, 2013b; del Río *et al.*, 2018), the age of the “Conglomerado osífero” is interpreted as late Miocene.

SYSTEMATIC PALEONTOLOGY

Class BIVALVIA Linnaeus, 1758
PALAEOHETERODONTA Newell, 1965
Order UNIONIDA Gray, 1854
Superfamily HYRIOIDEA Swainson, 1840
Family HYRIIDAE Swainson, 1840
Subfamily HYRIINAE Swainson, 1840
Tribe RHIPIDODONTINI Starobogatov, 1970

Genus *Diplodon* Spix in Wagner, 1827

Type species. *Diplodon ellipticus* Spix in Wagner, 1827; by OD. Rio São Francisco, Brazil.

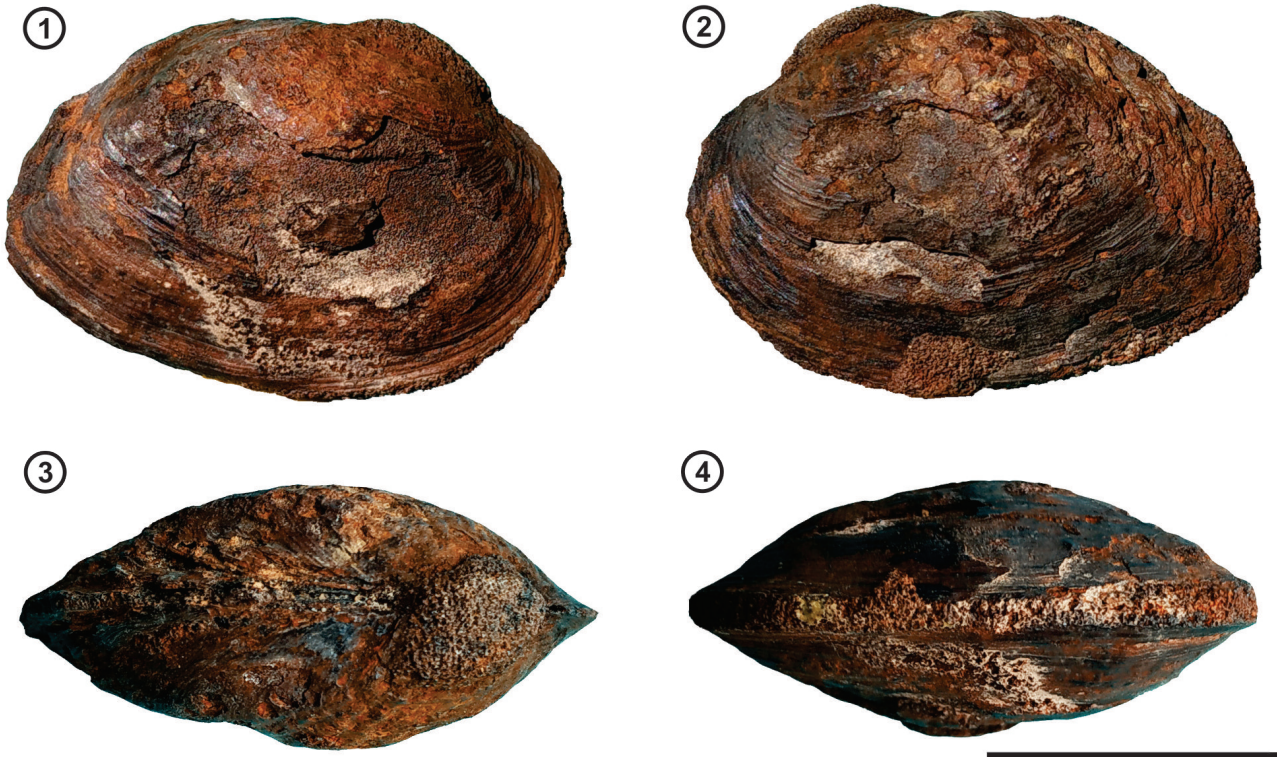


Figure 2. *Diplodon* sp. (DMT-Pi-536) in 1, right valve; 2, left valve; 3, dorsal margin; 4, ventral margin. Scale bar 20 mm.

Diplodon sp.

Figure 2.1–4

Material. DMT-Pi-536, one complete specimen with both valves articulated.

Geographic and stratigraphic occurrence. La Toma Vieja [31° 42' 09" S, 60° 28' 45" W], Paraná, Entre Ríos Province, Argentina; "Conglomerado osífero" (late Miocene).

Description. Shell medium to small sized, equivalve, inequilateral. The valves are subelliptic, somewhat laterally compressed, with rounded anterior margin and truncated posterior margin. The dorsal margin is slightly convex and the ventral margin curved. The umbo is prosogirous. The external surface is covered with slight commarginal lines and radially sculptured from the umbo downwards to about one third of the total height. There is a posterior carina, not very pronounced. Length: 39 mm, height: 26 mm, width: 17 mm.

Remarks. The specimen DMT-Pi-536 is considered to belong to the *Diplodon* genus because of its shape and the presence of ribs in the younger sector of the shell. This sculpture is a synapomorphy of Hyriinae (Graf & Cummings, 2006, 2007) that occurs in Australasia and South America (Graf *et al.*, 2015). Within this subfamily, three tribes are present in the Neotropical region: Hyriini, Castaliini, and Rhipidodontini, being the overall shape the only morphological difference among their genera (Parodiz & Bonetto, 1963; Miyahira *et al.*, 2019). In this sense, the specimen fits perfectly in the characterization of *Diplodon* made by Parodiz & Bonetto (1963: p. 199): "Shell regular in shape, not alate, always with radial ribs on the umbo, but of variable growth and posterior ridge scarcely developed, except in a few more elongated and more posteriorly acute forms, as in *Diplodon parallelipipedon* (Lea, 1834) or *D. parodizi* Bonetto, 1962". It is true that *Rhipidodonta* Mörch, 1853, can also be included in this definition. *Rhipidodonta* was considered traditionally as a subgenus of *Diplodon* (e.g., Parodiz & Bonetto, 1963; Haas, 1969), but other authors, such as Simone (2006) and Miyahira *et al.* (2017) elevated it to the generic rank. The difference between *Diplodon* and *Rhipidodonta* is the parasitic or non-parasitic condition of the glochidium, which obviously cannot be evaluated in this instance. In consequence, we have adopted the traditionally more in-

clusive name *Diplodon*. The shape and dimensions of the shell easily segregate *Diplodon* sp. from other nominal species found in the Neogene of Argentina (Fig. 3.1–2; Tab. 1).

The following specimens have been described from the Neogene of the Mesopotamian region: *Diplodon itapuensis* Morton & Sequeira, 1991, *Diplodon ituzaingoensis* Morton & Sequeira, 1991, and *D. aff. delodontus* (from Pliocene levels of the Ituzaingó Formation; Argentina and Paraguay) (Morton & Jalfin, 1987; Morton & Sequeira 1991). *Diplodon itapuensis* and *D. ituzaingoensis* are smaller than *Diplodon* sp. Additionally, *D. itapuensis* is more rounded, and although *D. ituzaingoensis* is somewhat elongated, it has a more posterior and less prominent umbo. *Diplodon aff. delodontus* is considerably larger than DMT-Pi-536 and more rounded.

Regarding other occurrences of Miocene *Diplodon* in more distant areas, Morton & Sepúlveda (1988) described *D. aff. colhuapiensis*, *D. aff. pehuenchensis*, and *D. aff. oponcitonis* from the Ñorquinco Formation. *Diplodon aff. colhuapiensis* is more elongated than our specimen and its umbo is more central and without sculpture. *D. aff. pehuenchensis* is also more elongated, it has a straighter ventral margin and has no umbonal structure. *Diplodon aff. oponcitonis* is subcircular and has a v-shaped umbonal sculpture.

Compared with DMT-Pi-536, *Diplodon colhuapiensis* Ihering, 1903 and *D. cf. colhuapiensis*, from the Santa Cruz Formation (Parodiz, 1969; Pérez *et al.*, 2019), are more elongated, have a less prominent and less inflated umbo and their dorsal and ventral margins are straighter. In addition, no umbonal sculpture is known for these taxa.

Diplodon rothi Ihering, 1904 from the Collón Curá Formation and *D. diluvii* (d'Orbigny, 1842) from the lower Pliocene of the Colorado river were redescribed by Parodiz (1969) and the latter species was studied by Griffin and Nielsen (2008). *Diplodon rothi* is very small and compressed with the umbo situated anteriorly and with a v-shaped sculpture. According to Parodiz (1969) the type specimen is immature. *Diplodon diluvii* is more elongated with a more centrally-located umbo that lacks any sculpture.

As was described above, the specimen DMT-Pi-536 has singular characteristics and it could represent a new species. Nevertheless, we have found only this unique exemplar, so we opt for maintaining it in open nomenclature.

TABLE 1. Dimensions of the Neogene species of *Diplodon* mentioned in the text. Measurements are expressed in mm.

Taxon	specimens	unit	length	height	width	Reference
<i>Diplodon</i> sp.	DMT-Pi-536	"Conglomerado osífero"	39	26	17	this paper
<i>D. contortus</i>	SMF 3906	Paraná Fm.	62	20	–	Parodiz (1969)
<i>D. itapuensis</i>	PZ-CTES 5246 (holotype)	Ituzaingó Fm.	31.5	26	12.6	Morton & Sequeira (1991)
<i>D. itapuensis</i>	Avg. 60 specimens	Ituzaingó Fm.	28.08	19.56	14.7	Morton & Sequeira (1991)
<i>D. ituzaingoensis</i>	PZ-CTES 5248 (holotype)	Ituzaingó Fm.	30	17	12	Morton & Sequeira (1991)
<i>D. ituzaingoensis</i>	Avg. 58 specimens	Ituzaingó Fm.	34.53	27.84	11.5	Morton & Sequeira (1991)
<i>Diplodon</i> A	PZ-CTES	Ituzaingó Fm.	103	71	–	Herbst & Camacho (1970)
<i>Diplodon</i> B	PZ-CTES	Ituzaingó Fm.	75	60	–	Herbst & Camacho (1970)
<i>D. aff. delodontus</i>	PZ-CTES 5089 avg 43 specimens	Ituzaingó Fm.	70.11	59.05	–	Morton & Jalfin (1987)
? <i>D. aff. delodontus</i>	PZ-CTES 7574, 7575.	San José Fm.	63	46	–	Morton & Herbst (2012)
<i>D. cf. colhuapiensis</i>	CM 61-137 (holotype)	Santa Cruz Fm.	51.5	30	18	Parodiz (1969)
<i>D. cf. colhuapiensis</i>	MACN-Pi 295	Santa Cruz Fm.	46.5	27	13.5	Pérez <i>et al.</i> (2019)
<i>D. cf. colhuapiensis</i>	MACN-Pi 296	Santa Cruz Fm.	44.5	24	14	Pérez <i>et al.</i> (2019)
<i>D. cf. colhuapiensis</i>	MPM-Pi 19425 avg. 5 specimens	Santa Cruz Fm.	76	43	25	Pérez <i>et al.</i> (2019)
<i>D. cf. colhuapiensis</i>	CM 61-137 (holotype)	Santa Cruz Fm.	52	30	19	Pérez <i>et al.</i> (2019)
<i>D. aff. colhuapiensis</i>	PZ-CTES 5094 avg 3 specimens	Ñorquinco Fm.	75	42	22	Morton & Sepúlveda (1988)
<i>D. aff. pehuenchensis</i>	PZ-CTES 5093 avg 3 specimens	Ñorquinco Fm.	75	46	15.5	Morton & Sepúlveda (1988)
<i>D. aff. oponcitonis</i>	PZ-CTES 5095 avg 2 specimens	Ñorquinco Fm.	70	53	18	Morton & Sepúlveda (1988)
<i>D. rothi</i>	CM (lectotype from lot 299 MACN)	Collon Cura Fm.	30	21	11	Parodiz (1969)
<i>D. diluvii</i>	CM 72654 (neotype)	lower Pliocene Colorado river	62	40	15	Parodiz (1969)
<i>D. diluvii</i>	s/n	lower Pliocene Colorado river	50	29	20	Parodiz (1969)
<i>D. diluvii</i>	s/n	lower Pliocene Colorado river	50	42	–	Parodiz (1969)
<i>D. diluvii</i>	s/n	lower Pliocene Colorado river	55	39	–	Parodiz (1969)
<i>D. diluvii</i>	s/n	lower Pliocene Colorado river	64	42	–	Parodiz (1969)
<i>D. diluvii</i>	CM 72654 (neotype)	lower Pliocene Colorado river	62.36	43	–	Griffin & Nielsen (2008)

Abbreviations: **Avg.**, average; **Fm.**, Formation.

DISCUSSION

In the Argentinean Mesopotamia, specimens of the family Hyriidae are widespread. The presence of the genera *Anodontites* (Bruguière, 1792), *Mycetopoda* (d'Orbigny, 1835), *Monocondylaea* (d'Orbigny, 1835), *Fossula* (Lea, 1870), *Leila*

(Gray, 1840), *Castalia* (Lamarck, 1819) and *Diplodon* (*vide supra*) (see Torres *et al.*, 2018) in the basins of the Paraná and Uruguay rivers (see Ageitos de Castellanos, 1960; Bonetto & Ezcurra de Drago, 1966; Scarabino & Mansur, 2007; Torres *et al.*, 2018), with a large number of living

species, denotes that the evolution of this group has been outstanding in this region. The few cases in which naiads appear mentioned in the fossil record of the Mesopotamian region, correspond to *Diplodon fraus*, supposedly from the Paraná Formation, Entre Ríos Province (see below), *Diplodon itapuensis*, *Diplodon ituzaiangoensis* and *D. aff. delodontus* were recovered from late Pliocene levels of the Ituzaiingó Formation in the Department of Itapúa (Paraguay) and in Corrientes Province of Argentina (Morton & Jalfin, 1987; Morton & Sequeira, 1991; Morton, 2004).

The only two records of *Diplodon* in the Paraná Formation of the Entre Ríos Province are highly questionable. The first one is a specimen originally described as *Modiola contorta* Borchert, 1901 (family Mytilidae), whose Holotype is deposited in the Senckenberg Museum, SMF 3906. Later it was named *Diplodon fraus* by Ihering (1907). Parodiz (1996) stated that it is an unnecessary combination and proposed the new name *Diplodon contortus* (Borchert, 1901) since *contorta* was not preoccupied in *Diplodon*. Parodiz (1969) stressed its similarity with *D. parallelopipedon* (Lea, 1834), a species currently living in the area. The only known specimens of *Modiola contorta* are those studied by Borchert (1901) and, since this collection is in great extent of unknown provenance, with specimens from the Quaternary and present, they probably do not belong to the Paraná

Formation (see Ihering, 1907; Frenguelli, 1920; Parodiz, 1969; Pérez, 2013a; Pérez *et al.*, 2013).

The other mention corresponds to a specimen analyzed by Joaquín Frenguelli, who, only based on the sediment attached to a putative *Diplodon*, inferred that the specimen could come from sandy levels similar to those found in the Calera Ozinalde area (Puerto Viejo, Paraná City) "...un trozo de material adherido a un ejemplar de *Diplodon fraus* lh., que debo a la amabilidad del profesor Martín Doello-Jurado" (...a fragment of material attached to a specimen of *Diplodon fraus* lh., which I owe to the kindness of Professor Martín Doello-Jurado) (Frenguelli, 1920, p. 127). In fact, the provenance of this specimen is unknown and the material was not properly described, figured, or kept in any collection. Thus, the presence of *Diplodon* among the fauna of the Paraná Formation was not properly recorded.

Considering the accurate records of *Diplodon* in the Mesopotamian region (i.e., *D. itapuensis*, *D. ituzaiangoensis*, and *D. aff. delodontus*), the presence of *Diplodon* sp. in the "Conglomerado osífero" at La Toma Vieja, Entre Ríos Province, extends the occurrence of the family Hyriidae at least to the latest Miocene of the region.

Present day unionids live in freshwater, being more frequent in lotic environments with moderate to somewhat fast current velocity, around 1 m deep, in firm to moderately

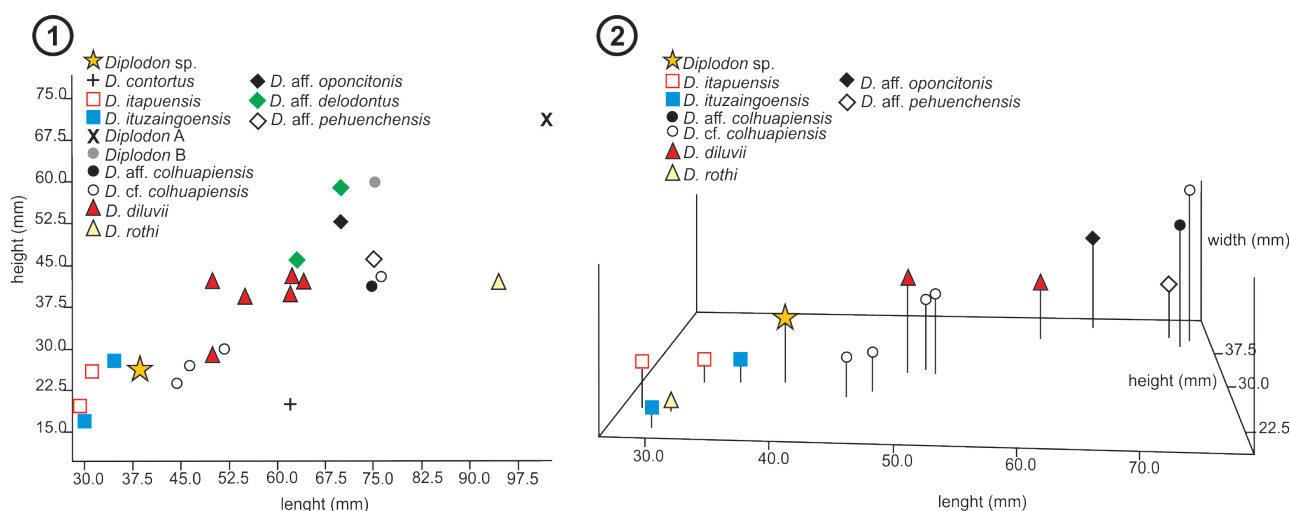


Figure 3. Dimensional relationships of the Neogene species of *Diplodon* referred in the text. 1, height /length; 2, height/ length/width. DMT-Pi-536 marked with a star. Measurements expressed in millimeters.

soft substrates with a wide range of clast sizes (Huehner, 1987; Dillon, 2004; Cummings & Graf, 2015). Additionally, species with large and heavy shells are found in water courses with relatively fast current, a hard substrate and coarse-grained sediment (Stanley, 1970; Bailey & Green, 1988; Cummings & Graf, 2015). According to the information synthesized in Miyahira *et al.* (2017), Rhipiodontini live in lotic and lentic environments, but are rare in strong currents. They prefer, but are not limited to, a fine-grained substrate rich in organic content. In consequence, they are not usually present in headwaters, but in the more distal parts of the rivers.

As was indicated above, several authors (*e.g.*, Frenguelli, 1920; Aceñolaza, 1976, 2000; Brunetto *et al.*, 2013) considered the “Conglomerado osífero” as part of the fluvial deposits of the Ituzaingó Formation. Moreover, Brunetto *et al.* (2013) regarded it as part of the lower member of the Ituzaingó Formation. In this sense, the “Conglomerado osífero” would correspond to a continental paleoenvironment dominated by a fluvial system. However, Pérez (2013a) considered the “Conglomerado osífero” as part of a paleoenvironment dominated by fluvial channels with tidal influence, and concluded that these levels correspond to the Paraná Formation (marine in origin). In this scenario, and although not being conclusive about the depositional environment, the presence of *Diplodon* sp., a freshwater Rhipiodontini, in the “Conglomerado osífero”, would support the traditional idea of a continental paleoenvironment dominated by a fluvial system with low energy and firm or moderately soft substrates, composed of fine-grained sediment.

SUMMARY

The first accurate fossil record of *Diplodon* for Entre Ríos Province is presented herein. The finding of *Diplodon* sp. in the “Conglomerado osífero” extends the temporal distribution of the genus in Mesopotamian region until at least the latest Miocene. Although the conglomerate lenses that contain these Neogene deposits would have a mixed contribution of taxa of freshwater and marine paleoenvironments, the finding of this specimen would support the traditional interpretation of a continental paleoenvironment dominated by a fluvial system.

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